

## RESEARCH ARTICLE

## Temporal and inter habitat variations of substratum, vegetation and substratum macroinvertebrates attributes across coastal wetland systems, North East Aegean, Greece

Dikou Angela<sup>\*1</sup>, Evaggelatos Krystalia.<sup>1</sup>, Dinapoya Vaia<sup>1</sup>, Lambrianidis Epaminondas<sup>1</sup>, Agiannidis Costas<sup>1</sup>, Koutsofta Panayiota<sup>1</sup>, Perakis Nikos<sup>1</sup>, Sigüero Arsinoe<sup>2</sup>, Stylianou Skevi<sup>1</sup>, Bazos Yioannis<sup>1</sup>, Iatrou Giorgos<sup>1</sup>, Troumbis Andeas<sup>1</sup>.

<sup>1</sup> Department of Environment, University of the Aegean.

<sup>2</sup> Department of Science, Universidad Autonoma de Barcelona.

\*Corresponding author: Phone +30 24210 93259, Fax: +30 24210 93157, E-mail [angeladikou@hotmail.com](mailto:angeladikou@hotmail.com)

### Abstract

- 1 - Using five coastal wetland systems across Kalloni bay, Lesbos Island, NE Aegean, we investigated: (I) the interaction between spatial units (land, wetland, sea) and seasons (spring, autumn) of substratum physicochemical attributes, vegetation composition and aerial cover, and substratum macroinvertebrates distribution and abundance and (II) the relative importance of substratum attributes in explaining temporal and inter habitat variations in vegetation and substratum macroinvertebrates distributions to elucidate the functional role of these coastal wetlands in the landscape.
- 2 - Electrical conductivity, percent organic matter and bulk density of substratum showed the most pronounced differences among spatial units, between seasons, and among spatial units x seasons interaction, respectively. Comparison of C:N and N:P ratios among spatial units and between seasons indicated that, in general, nitrogen and phosphorus appear to be limiting factors at the sea and the land unit, respectively. It is likely that these coastal wetlands function as transformers of chemical elements while P limits primary production.
- 3 - Significant substratum physicochemical attributes explained 23.4 and 14.7% of plants distribution in spring (percent organic matter, total phosphorus concentration, electrical conductivity) and autumn (electrical conductivity, pH), respectively, while significant substratum variables explained 46.1 and 73.3% of macroinvertebrates distribution in spring (percent organic matter) and autumn (total phosphorus concentration, electrical conductivity, percent organic matter), respectively.

**Keywords:** coastal wetlands, Mediterranean, substratum correlates, plants and soil macroinvertebrates, spatial and temporal patterns

### Introduction

Coastal wetlands, namely lagoons, tidal, freshwater, and estuarine marshes, are considered as transitional ecosystems that regulate temporally variable fluxes of materials and energy between the land and the sea (through the movement of water and organisms), provide important services to humans (coastal defense, wildlife conservation, maintenance of water quality, spawning and nursery grounds for fish and

crustaceans, recreation), and are particularly vulnerable to global change (due to sea level rise and alterations in precipitation patterns) (Vernberg, 1993; Boorman, 1999; Mitch and Gosselink, 2000; Levin *et al.*, 2001; Wall *et al.*, 2001; Adam, 2002; Valiela *et al.*, 2004; Cattrijsse and Hampel, 2006; Lotze *et al.*, 2006). Coastal wetlands of the NE USA (Teal, 1962; Day *et al.*, 1973; Woodwell *et al.*, 1977; Dame *et al.*, 1986; Correll *et al.*, 1992), NW France and the Netherlands (Lefeuve *et al.*,

2000) seem to function as exporters of organic matter to adjacent marine waters while those of the Wadden Sea (Bakker *et al.*, 1993) as nitrogen transformers. There are only few studies, however, that describe spatial structure (sea/coastal wetland/upland: Dikou *et al.*, 2008; coastal wetland/upland: Álvarez Rogel *et al.*, 2001) or temporal dynamics (coastal wetland/sea: Lefeuvre *et al.*, 2000; Pérez-Ruzafa *et al.*, 2008) of abiotic and/or biotic components across the land, wetland, and sea units of coastal wetland systems in the Mediterranean. Such an approach is indispensable for the elucidation of their functional role in the landscape.

Using five coastal wetland systems across Kalloni bay, Lesvos Island, NE Aegean, we compared seasonal patterns of substratum physicochemical attributes, vegetation cover, and substratum macroinvertebrates abundance. Coastal wetlands of Kalloni bay, Lesvos Island, NE Aegean, constitute an ecological network, which has been incorporated into the European Network of protected areas Natura 2000 (GR4110004; Mandylas and Kardakari, 1998), the list of CORINE biotopes, the list of important areas of avian fauna of Greece (SPPE), and the 20 national Ecological Hot Regions (Hotspots) for avian fauna (Troumbis and Dimitrakopoulos, 1998). They are characterized by intermitted hydroperiod during the dry summer and they receive

water mainly through rainfall and to a lesser degree through the high underwater table and the sea. Specifically we attempted to answer the following questions: 1) Do substratum physicochemical properties, vegetation cover, and substratum macroinvertebrate abundances differ between seasons (spring, autumn) and among units (sea, wetland, land)? 2) Which substratum properties best relate with/explain spatial and temporal distributions of plants and substratum macroinvertebrates across the coastal systems studied?

## Materials and Methods

### Sampling

The five wetlands studied (Apothika estuarine lagoon, Parakoila swamp, Kalloni salt meadow, Vouvaris estuarine lagoon, and Polihnitos salt pan) develop on an alluvial flat plain of mineral soils along Kalloni bay, Lesvos Island, NE Aegean, Greece and are described in Dikou *et al.* (2008).

At each wetland system there was one station at sea, one station within the wetland, and one station on land. Distance of sampling stations (15 stations, 3 units x 5 coastal wetland systems) from the coast is given in Table 1. At each station, five surface (0-2 cm) substratum samples were scooped, dried in room temperature, crashed and sieved through 2 mm mesh size sieve. These samples were used to determine attributes of the structure

Table 1. Distance of sampling stations from the intertidal zone across the five coastal wetland systems of Kalloni bay studied. Percentages of sand, silt and clay in brackets.

COASTAL SYSTEMS	STATIONS WITHIN SPATIAL UNITS		
	Sea (m)	Wetland (m)	Land (m)
Apothika	0 [70.0, 3.2, 26.8]	200 [54.3, 10.0, 35.7]	500 [35.6, 9.6, 54.8]
Parakoila	0 [54.2, 12.7, 33.1]	200 [16.9, 18.3, 64.8]	450 [89.0, 0.6, 10.4]
Kalloni	0 [89.0, 1.2, 9.8]	200 [64.0, 6.0, 30.0]	350 [49.0, 12.2, 38.8]
Polyhnitos	0 [81.2, 3.0, 15.8]	200 [26.3, 11.4, 62.3]	350 [44.2, 14.1, 41.7]
Vouvaris	0 [85.0, 4.9, 10.1]	150 [33.7, 14.1, 52.2]	200 [48.3, 9.6, 42.1]

(Bulk Density, BD; texture), chemistry (Electrical Conductivity, EC; pH) and production (Total Phosphorus concentration, TP; Total Nitrogen concentration, TN; percent Organic Matter, OM; C:N ratio; N:P ratio) of the substratum. Bulk density of substratum samples was measured after drying at 1000 C for 24 hours of steady soil/sediment sample volume (40.10 cm<sup>3</sup>; brass ring liner of core sampler), weighting, and dividing their weight by the steady volume. Texture as percent composition of sand, silt and clay was determined using Bouyoukos method (Allen, 1989). Electrical conductivity and pH were measured in saturated solutions of 1:5 soil to water ratio, after centrifugation and filtration through 47 mm filters, with the use of a portable electrometric unit Consort 932. Total phosphorus concentration was measured using Olsen's method (Olsen *et al.*, 1954). Total nitrogen concentration was measured using wet Kendjal's method (Bremner and Mulvaney, 1982). Percent organic content was measured with the method of wet oxidation.

At each station, another five surface (0-2 cm) substratum samples (250 cm<sup>3</sup> volume) were scooped and placed in self-sealing plastic bags. They were then left to dry at room temperature, crashed, and examined using magnifying lenses for the presence of macroinvertebrates (whole individuals or parts of them). Animals were stored in vials containing ethanol, sorted, identified and counted. Substratum macroinvertebrates were classified at class level.

We obtained specimens and recorded areal cover of all plants encountered under three adjoining 1 m<sup>2</sup> quadrats at each station. After sampling, plant specimens were preserved by drying and identified under stereoscope with the use of identification keys and guides. Sampling took place at the same stations during March and September 2005.

### *Statistical analysis*

Significant differences in (transformed) substratum variables among spatial units (sea, wetland and land), between seasons (spring, autumn) and their interaction (unit x season) were tested using a 2-way repeated measures ANOVA. Post-hoc, pair-wise comparisons were tested using Tukey's HSD test. Effect size of main effects and their interaction was based on partial eta squared.

The aforementioned univariate tests were performed using SPSS 12.0. Significant differences in mean percent cover of plant species and in mean abundance of substratum macroinvertebrate taxa among units were tested with one-way ANOSIM and 2-way crossed ANOSIM, respectively using PRIMER 5.0.

Canonical Correspondence Analysis (CCA) of CANOCO 4.5 was used to analyze the spatial distribution of plant (based on areal cover) and substratum macroinvertebrate (based on abundances) taxa in relation to substratum variables both in spring and autumn. Analyses were undertaken on the 15 stations. CCA classified the substratum variables, beginning with the one that extracted the greatest amount of the variance in the species data matrix. Significant factors entering final analysis were selected based on conditional effects (Lepš and Šmilauer, 2003).

The robustness of the final analysis was determined using a Monte Carlo permutation test. To reveal statistically significant pair-wise relationships between plant, substratum macroinvertebrate taxa and substratum variables (i.e. which taxon depends on which substratum variable) we employed t-value biplots (Lepš and Šmilauer, 2003). These diagrams contain arrows for the taxa, arrows for the substratum variables, and projections of the tips of the arrows of the substratum variables, each forming a cycle

overlying taxa arrows. Taxa arrows that end within a cycle have a statistically significant and positive regression coefficient for the respective substratum variable with a corresponding t-value larger than 2.0. Analogous conclusions can be drawn for the cycle going on the opposite direction but, in this case, the relationship is negative.

To depict the degree of separation based on taxa composition of plants (based on areal cover) and substratum macroinvertebrates (based on abundances), diagrams with sample scores were plotted for each season.

The separation among spatial units was shown with different symbol types for each unit and corresponding envelopes enclosing all samples belonging to a particular spatial unit.

## Results

### *Spatial and temporal patterns of abiotic and biotic components*

Patterns of variation across sea, wetland and land units differed between seasons for all substratum variables examined (Figure 1, Table 2).

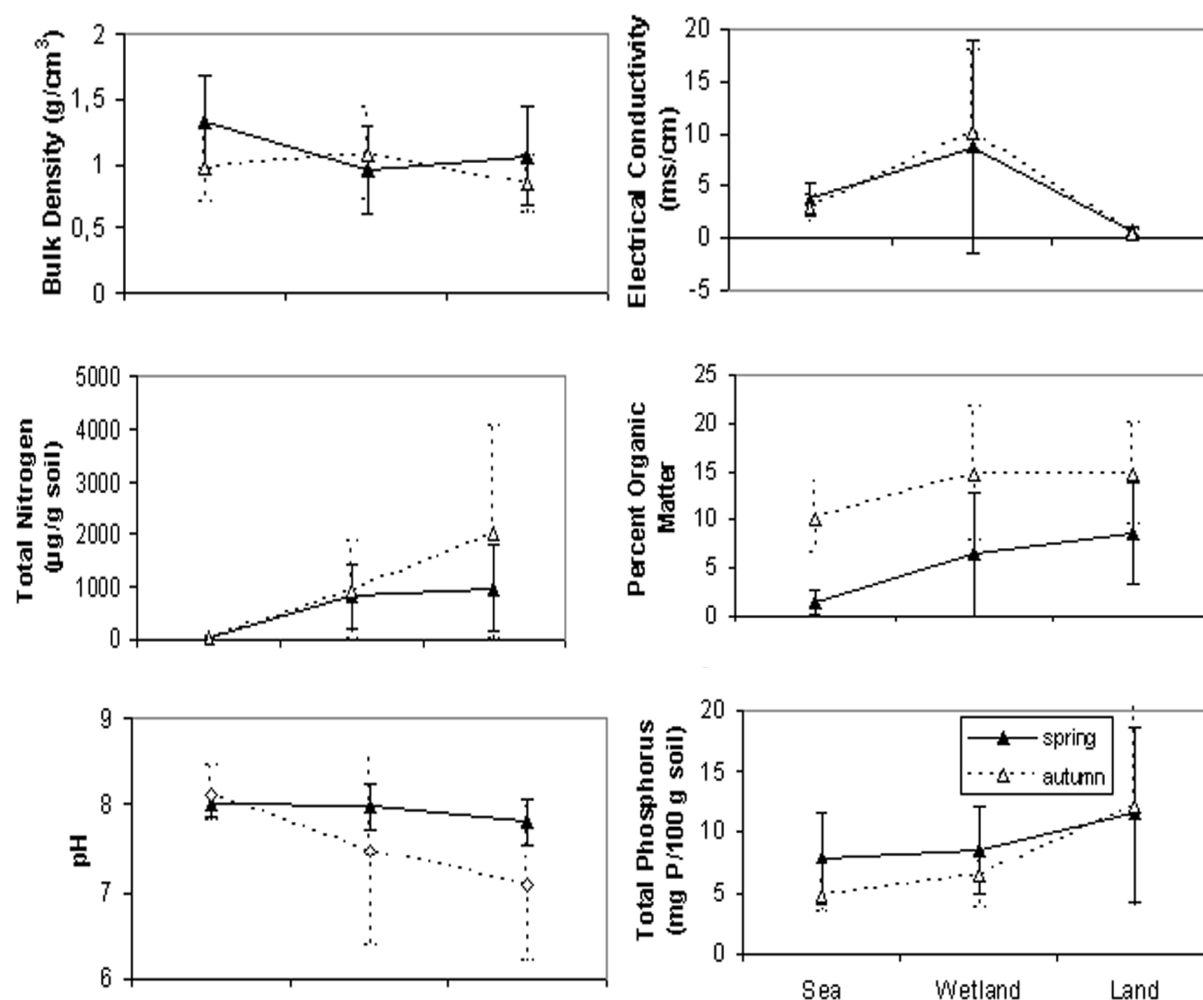


Figure 1 - Spatial variation (mean±stdev) in substratum properties across five coastal wetland systems of Kalloni bay, in spring and autumn of 2005, N=25.

Table 2. Results of post-hoc pair-wise comparisons for all combinations of the levels of main factors (units: sea, wetland, land; seasons: spring, autumn) using Tukey's HSD test. Bulk Density: ■; log(Electrical Conductivity): □; arcsin(pH): ●; (Total Phosphorus)<sup>0.223</sup>: ○; double square root(Total Nitrogen): ▣; square root(Percent Organic Matter): ▤.

		SEA		WETLAND		LAND	
		SPRING	AUTUMN	SPRING	AUTUMN	SPRING	AUTUMN
SEA	SPRING						
	AUTUMN	■ ○ ▤					
WETLAND	SPRING	■ ▣ ▤	□ ○ ▣ ▤				
	AUTUMN	■ □ ▣ ▤	□ ● ○ ▣	□ ○ ▤			
LAND	SPRING	■ □ ○ ▣ ▤	□ ● ○ ▣	□	□ ○ ▤		
	AUTUMN	■ □ ● ○ ▣ ▤	□ ● ○ ▣ ▤	□ ● ○ ▣ ▤	■ □ ● ○ ▣	■ ● ▣ ▤	

In spring, percent organic matter, total nitrogen concentration, and electrical conductivity showed significantly lower values at sea compared to wetland and land units; total phosphorus had significantly lower concentrations at sea and wetland compared to land units; bulk density had significantly higher values at sea compared to wetland and land units; pH remained fairly stable across the different units. In autumn, total phosphorus concentration, total nitrogen

concentration, and percent organic matter increased progressively and significantly from the sea, through the wetland and towards the land unit; pH decreased progressively and significantly from sea through wetland and towards land units; electrical conductivity showed peaks within wetland units; bulk density was significantly lower at the land unit compared to the wetland unit. Electrical conductivity, percent organic matter, and bulk density showed the most pronounced

differences among units, between seasons, and for the unit x season interaction, respectively (Table 3).

coastal wetland systems were considered (Figure 2). Both in spring and autumn, the lowest N:P ratios appeared at the sea (11:1

Table 3. Effect size (partial eta squared) for main effects (units, seasons) and their interaction (unit x season). EC: electrical conductivity, TP: total phosphorus concentration, TN: total nitrogen concentration, OM: percent organic matter.

	BD	log(EC)	arcsin(pH)	TP <sup>0.223</sup>	dsqrt(TN)	sqrt(OM)
units	0.086	0.802	0.278	0.209	0.688	0.355
seasons	0.221	0.004	0.031	0.263	0.048	0.721
unit x season	0.318	0.221	0.192	0.233	0.149	0.185

In spring, the highest and the lowest C:N ratios appeared at the sea (556:1) and at the wetland (83:1) unit, respectively. Also, in autumn the highest C:N ratios appeared at the sea (6134:1) unit while the lowest C:N ratios appeared at the land (164:1) unit. C:N ratios were higher in autumn compared to spring for all spatial units when all five

and 0.4:1, respectively) unit. The highest N:P ratios appeared at the wetland (14:1) unit in spring and at the land (32:1) unit in autumn (Figure 2).

Fifty and fifty three plant species were encountered under three adjacent, 1 m<sup>2</sup> replicate quadrats at the sea, wetland and land units of the five coastal wetland systems

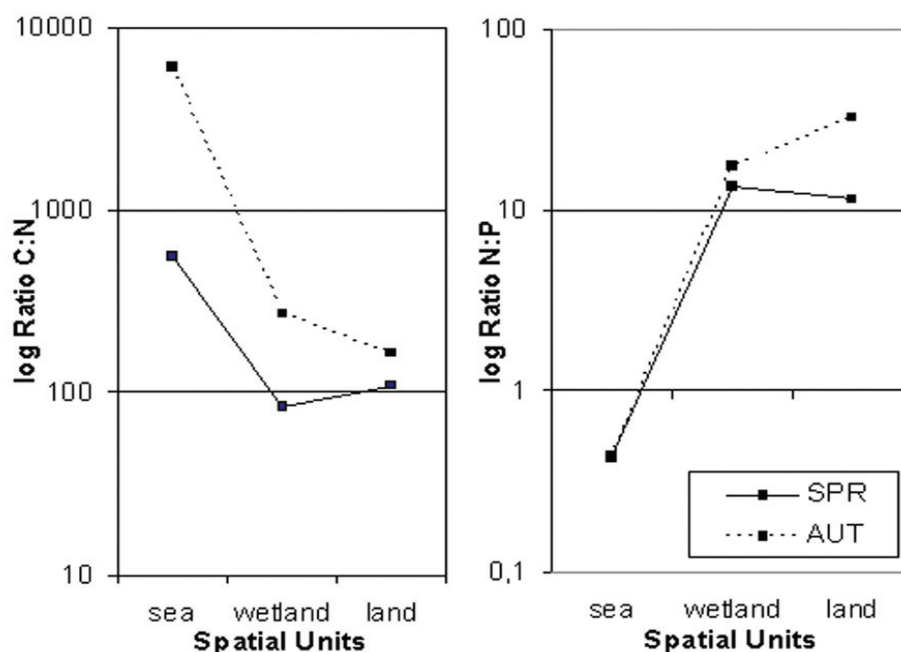


Figure 2 - Spatial and seasonal variation in C:N and N:P ratios of substratum, N=25.

studied in spring and autumn, respectively (Appendix A). Although we were not able to identify all specimens to species level, we are fairly sure that there was no species in common found between spring and autumn samplings (except possibly for species no. 6 and 55 of Appendix A).

Also, each spatial unit had distinct floral compositions; the angiosperm *Cymodocea nodosa* and marine algae appeared within the sea units; halophytes, such as the genus *Arthrocnemum*, appeared within wetland stations; species of the families Graminae

way ANOSIM Global  $R=0.346$ ,  $p=0.05$ ).

Distribution and abundance of substratum macroinvertebrate taxa indicated that gasteropoda and bivalvia dominated at sea units while insecta dominated at land units both in spring and autumn (Figure 3). There were significantly higher mean total abundances of substratum macroinvertebrates at the sea unit compared to wetland and land units (when both seasons were grouped) (two-way crossed ANOSIM Global  $R=0.402$ ,  $p=0.01$ ). However, there was no statistically significant difference in mean total

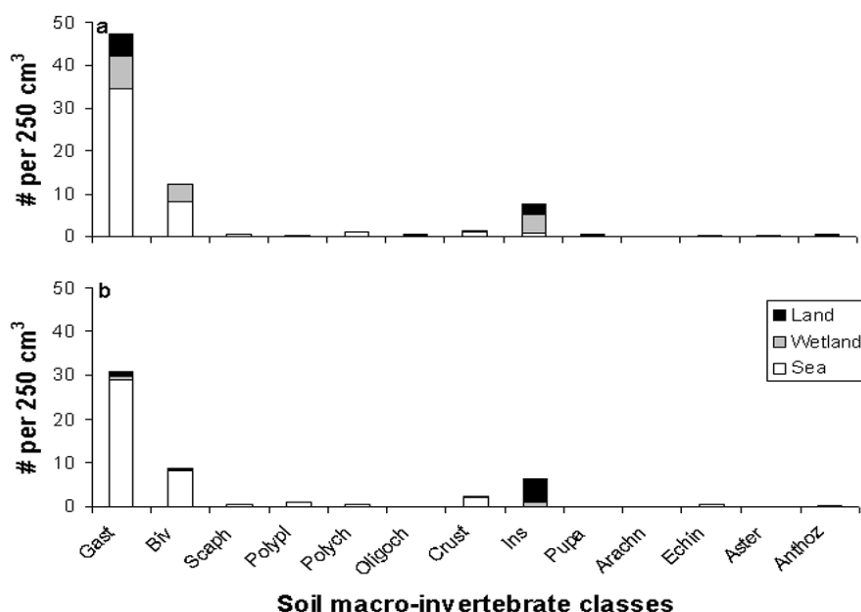


Figure 3. Mean density of substratum macroinvertebrate taxa among sea, wetland and land units of five coastal wetlands (N=5) in: a) spring and b) autumn of 2005. Gast: gasteropoda, Biv: bivalvia, Polypl: polyplacophora, Polych: polychaeta, Oligoch: oligochaeta, Crust: crustacean, Ins: insecta (mature), Pupa: insecta (immature), Arach: arachnidae, Echin: echinodermata, Aster: asteroidea, Anthoz: anthozoan.

and Compositae prevailed on land. There was significantly higher mean percent areal cover of plant species on land compared to wetland and sea units in spring (one-way ANOSIM Global  $R=0.378$ ,  $p=0.04$ ) and autumn (one-

abundances of substratum macroinvertebrates between seasons (when spatial units were grouped) (two-way crossed ANOSIM Global  $R=-0.078$ ,  $p=0.90$ ).

Spatial units presented substantial overlap in



spring but differentiated well in autumn when both plant and substratum macroinvertebrate compositions were considered (Figure 4).

distribution of substratum macroinvertebrate taxa correlated significantly with percent organic matter in spring (46.1% of variance

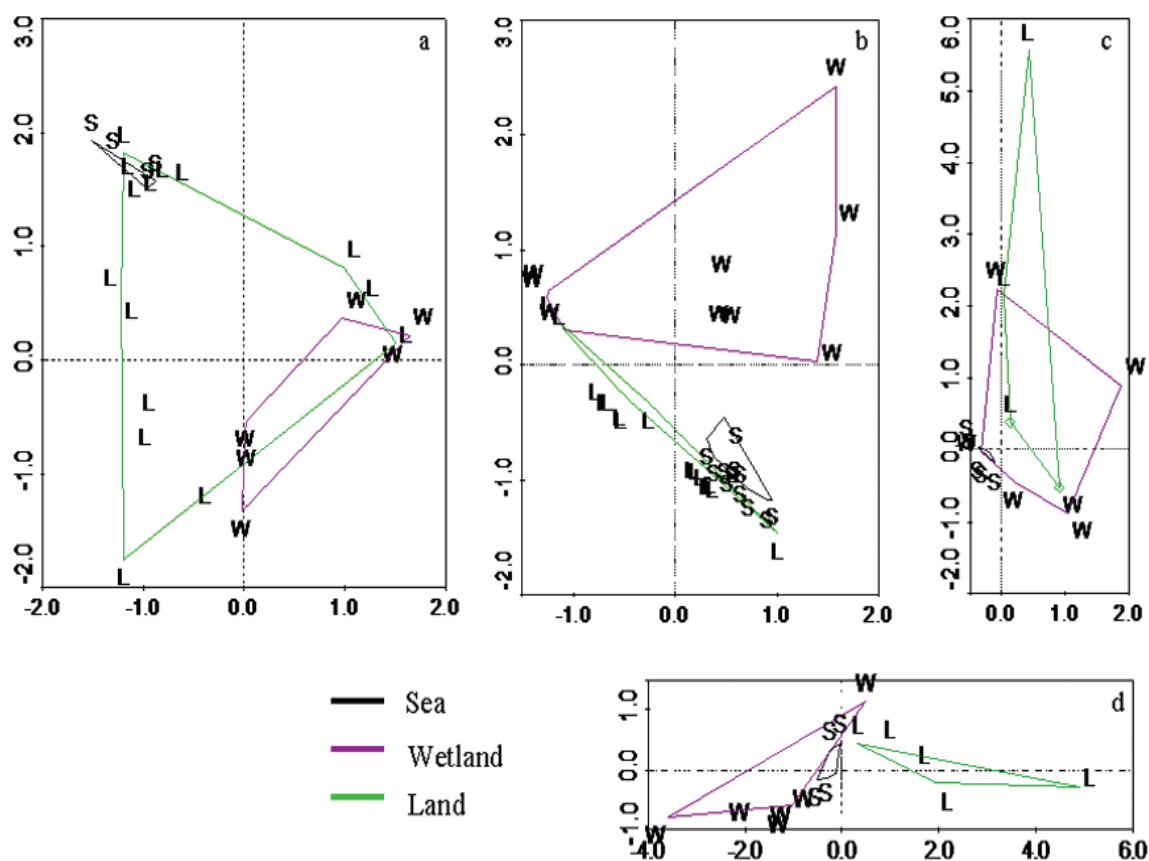


Figure 4 - Samples scatterplots based on areal cover of plant species in spring (a) and autumn (b) and on mean total abundance of substratum macroinvertebrate taxa in (c) spring and (d) autumn. Separation among spatial units (sea, wetland, land) is shown with envelopes enclosing all samples of a particular spatial unit.

#### *Abiotic correlates of biotic patterns*

The results of CCA performed on plant and substratum macroinvertebrate community compositions in spring and autumn are presented in Table 4. The distribution of plants was significantly correlated with percent organic matter, total phosphorus concentration and electrical conductivity in spring (23.4% of variance explained) and with electrical conductivity and pH in autumn (14.7% of variance explained). The

explained) and with total phosphorus concentration, electrical conductivity and percent organic matter in autumn (73.3% of variance explained). The aforementioned substratum variables were correlated with ordination axes at different degrees (Table 4).

Examination of t-value biplots showed that a number of plant and substratum macroinvertebrate taxa exhibited positive or negative relationships with the significant



substratum variables in spring and autumn (Table 5). In spring, *Veronica* sp., *Matricaria chamomilla*, *Urtica membranacea* and an unidentified species (no. 20 of Appendix A) showed significant positive relationships with both total phosphorus concentration and electrical conductivity; another unidentified

species (no. 31 of Appendix A) showed significant negative relationships with percent organic matter, total phosphorus concentration and electrical conductivity; *Cardus/Echinops* sp. showed significant positive relationship with percent organic matter and significant negative relationship

Table 4. Summary of CCA performed on the areal cover of plant species and on the abundance of substratum macroinvertebrate taxa in spring and autumn. Conditional effects were obtained from the summary of forward selection in order to select significant substratum variables.

PLANTS Spring						
	Conditional effects			Correlations of environmental factors with ordination axes		
	Lambda A	p	F	Axis 1	Axis 2	Axis 3
(1) OM	0.91	0.002	2.17	0.91	-0.29	-0.17
(2) TP	0.84	0.004	2.10	-0.49	-0.66	-0.44
(3) EC	0.78	0.060	2.02	0.01	-0.43	0.75
<i>Summary statistics for ordination axes</i>						
Eigenvalues				0.924	0.901	0.706
Species-environment correlations				0.98	0.95	0.84
Sum of unconstrained eigenvalues					10.832	
Sum of canonical eigenvalues					2.530	
Cumulative percentage variance of species data					23.40	
Probability associated with Monte Carlo tests					0.002	
PLANTS Autumn						
(1) EC	0.84	0.002	2.93	0.66	0.70	
(2) pH	0.65	0.004	2.34	0.95	-0.25	
<i>Summary statistics for ordination axes</i>						
Eigenvalues				0.98	0.81	
Species-environment correlations				0.99	0.93	
Sum of unconstrained eigenvalues					12.178	
Sum of canonical eigenvalues					1.791	
Cumulative percentage variance of species data					14.70	
Probability associated with Monte Carlo tests					0.002	
MACROINVERTEBRATES Spring						
(1) OM	0.33	0.008	4.02	0.68		
<i>Summary statistics for ordination axes</i>						
Eigenvalues					0.327	
Species-environment correlations					0.680	
Sum of unconstrained eigenvalues					1.303	
Sum of canonical eigenvalues					0.327	
Cumulative percentage variance of species data					46.10	
Probability associated with Monte Carlo tests					0.008	

MACROINVERTEBRATES Autumn						
(1) TP	0.49	0.004	9.50	0.71	-0.32	0.11
(2) EC	0.16	0.018	3.80	-0.49	-0.28	0.29
(3) OM	0.11	0.036	3.29	0.40	0.49	0.24
<i>Summary statistics for ordination axes</i>						
Eigenvalues				0.641	0.071	0.013
Species-environment correlations				0.828	0.751	0.415
Sum of unconstrained eigenvalues					1.156	
Sum of canonical eigenvalues					0.725	
Cumulative percentage variance of species-environment relation					73.3	
Probability associated with Monte Carlo tests					0.002	

with total phosphorus concentration. In autumn, *Cymodocea nodosa* and an unidentified species (no. 52 of Appendix A) showed significant positive relationships with pH and significant negative relationships with electrical conductivity; *Arthrocnemum macrostachyum* showed significant negative relationships with both electrical conductivity and pH. In spring, arachnidae and insecta showed significant positive relationships with percent organic

matter while gasteropoda and echinoderata showed significant negative relationships with the same substratum variable. In autumn, insecta showed significant positive and negative relationships with total phosphorus concentration and electrical conductivity, respectively; polychaeta, anthozoa and crustaceans showed significant negative relationships with total phosphorus concentration and significant positive relationships with percent organic matter.

Table 5. Results of evaluation for significance of relationships of (a) areal cover of plant species and (b) abundance of substratum macroinvertebrate taxa with significant substratum variables based on t-value biplots. Plant species numbers correspond to species ids in Table 4. OM: percent organic matter; TP: total phosphorus concentration; EC: electrical conductivity.

relationship	Spring			Autumn	
	OM	TP	EC	EC	pH
positive	11, 5	6, 16, 18, 19, 20, 21, 22, 23	19, 20, 21, 23, 27		51, 52, 86, 87
negative	20, 28, 29, 30, 31, 32	5, 31, 37	30, 31	51, 52, 55, 58	55, 60, 61, 62, 63, 67

relationship	Spring		Autumn	
	OM	OM	EC	TP
positive	insecta, arachnidae	polychaeta, crustaceans	anthozoa	insecta
negative	gasteropoda, echinodermata		insecta	gasteropoda, polychaeta, anthozoa crustaceans

## Discussion

Among the substratum attributes studied, electrical conductivity and percent organic matter were primarily responsible for the distinction among the sea, wetland and land units of the five coastal wetland systems studied and for the distinction between seasons, respectively. Electrical conductivity was significantly higher in wetland unit compared to land and sea units and significantly higher at the sea compared to the land unit both in spring and autumn. However, it was only at the wetland unit that electrical conductivity was significantly higher in autumn compared to spring. Seasonal variations in soil salinity have been attributed to alternating periods of rainfall, during which salts are leached towards the deepest soil horizons and periods of drought when they are brought to the surface horizons (Álvarez Rogel, 2000). In addition, evaporation periods are longer at higher elevations and thus salts in surface soils may become more concentrated (Silvestri *et al.*, 2005).

Percent organic matter was significantly higher in autumn (end of growing season) than spring (end of winter) at all three spatial units examined, i.e. sea, wetland and land. It was also significantly higher on land compared to wetland and significantly higher in wetland compared to sea. It has been speculated that due to their irregular inundation only during the highest tides, European marshes' export of organic material is largely absent (Boorman, 1999; Cattirjse and Hampel, 2006). Among the five coastal wetlands studied, Polihnitos and Apothika receive seawater directly and periodically; Vouvaris receives limited volume of seawater or less frequently; and Kalloni and Parakoila, are influenced by brackish groundwater and salt infusion. Thus, the coastal wetlands studied must probably be functioning as

transformers of organic matter (Mitch and Gosselink, 2000).

Comparison of C:N and N:P ratios among spatial units and between seasons showed the relative importance of nitrogen and phosphorus, respectively, as limiting factors of primary production (Boorman, 1999). It appears, that, in general, N and P appear to be the limiting factors at the sea and the land unit, respectively, both in spring and autumn. Nitrogen and phosphorus follow different pathways in ecosystems (Gächter *et al.*, 2004) and factors that dictate whether nitrogen or phosphorus limits production are linked not to whether a system is aquatic or terrestrial but rather to characteristics, such as the nature of external nutrient fluxes, underlying geological substrate, and biotic characteristics (Grimm *et al.*, 2003).

Abundances of substratum macroinvertebrates recorded in this study were quite low compared to values of a few thousand individuals per m<sup>2</sup> obtained within comparable coastal wetlands elsewhere, including the Mediterranean region (Els Alfacs shallow-water bay, Ebre Delta, NE Spain, Palacín *et al.*, 1991; southern New England salt marsh, Sardá *et al.*, 1995; intertidal, soft-sediment estuary, Schelde estuary, Netherlands, Ysebaert and Herman, 2002). Also, total macroinvertebrate abundances did not differ between spring and autumn contrary to the generalized seasonal pattern established in temperate zones with a peak from late spring to early summer (in Sarda *et al.*, 1995). Physiological stress related to increased salinity and desiccation may be responsible for both the relatively low abundances and lack of a seasonal pattern of variation in surface substratum macroinvertebrates found in this study. There was distinct, however, seasonality in vegetation composition at all spatial units examined. Yet, contrary to substratum macroinvertebrate abundances,

which peaked within the sea unit, percent areal cover of vegetation peaked within the land unit.

The substratum attributes examined in this study explained a large percentage of variation in substratum macroinvertebrate distributions but a relatively small percentage of variation in vegetation distributions across the five coastal wetland systems in both seasons. Also, six plant species and insecta showed significant negative relationships with electrical conductivity while five plant species showed significant positive relationships with electrical conductivity. Furthermore, two plant species along with arachnidae, insecta, polychaeta, crustacean and anthozoa showed significant positive relationships with percent organic matter while six plant species along with gasteropoda and echinodermata showed significant negative relationships with percent organic matter.

The study revealed distinctive differences in structure and function of coastal wetlands in NE Mediterranean compared to relevant studies in other European coastal wetlands. It is likely that these coastal wetlands function as transformers of chemical elements while P limits primary production. Percent organic

matter and electrical conductivity may be important substratum properties when monitoring spatial and temporal dynamics across these coastal wetland systems; both variables showed significant differences among spatial units and between seasons and were also significantly correlated with a number of plant and substratum macroinvertebrate taxa across the land/coastal wetland/sea gradients. High salinity and desiccation may be responsible for comparatively low abundances of substratum macroinvertebrate taxa.

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